The distribution, abundance and vulnerability to population reduction of a nomadic nectarivore, the Grey-headed Flying-fox *Pteropus poliocephalus* in New South Wales, during a period of resource concentration

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ABSTRACT

The Grey-headed Flying-fox *Pteropus poliocephalus* has an expansive range. However, the species actually occupies a relatively restricted and continuously changing habitat area, which is primarily defined by irregular patterns of nectar availability. A synchronous count of Grey-headed Flying-foxes in New South Wales taken in July 1998 described the distribution and abundance of the species during a time of general food scarcity, but when abundant floral resources were available in restricted patches of coastal vegetation. The population was highly concentrated into small habitat areas associated with this flowering. The species occupied 11 camps which were located at irregular intervals along the coast, north from the Sydney region. Over 99% of the New South Wales population occurred in nine camps. The total abundance of animals in the state was estimated at 85 400. These results vary substantially from recent estimations which placed the size of the New South Wales population at one million animals. Black Flying-foxes occupied seven camps at the time of the count and their abundance was estimated at 72 500. Periods of concentration are periods of vulnerability for migratory species and present appropriate circumstances in which to examine their conservation status. Critical winter habitat used by Grey-headed Flying-foxes at the time of this study is poorly reserved, primarily occurs on privately-owned land and is located in areas targeted for urban and rural residential development to cater for an ongoing, rapid increase in human population. The conclusion drawn from this study was that Grey-headed Flying-foxes are vulnerable to population decline from the ongoing clearing of their critical over-wintering habitat in lowland coastal vegetation in north-east New South Wales and south-east Queensland. These results support their listing as Vulnerable in the *1999 Action Plan for Australian Bats*.

Key words: Flying-foxes, *Pteropus poliocephalus*, Conservation, Migration, Nomads, Endangered species, New South Wales.

INTRODUCTION

Various life history characteristics of migratory animals make it difficult to incorporate their needs into conservation strategies and monitor their threatened status (Myers *et al.* 1987; Brower and Malcolm 1991; Pagel and Payne 1996; Friesen 1997). This is particularly true of mobile taxa which move between ephemeral resource flushes and whose movement patterns are therefore irregular, difficult to define and at least partially nomadic (Woinarski *et al.* 1992; Frederick *et al.* 1996). Complex patterns of habitat use by nomads inhibit our capacity to estimate the parameters commonly used to assess conservation status, such as levels and trends of abundance, distribution of critical habitat, shifts in habitat quality, reproductive capacity and reproductive lifespan. They also bring into serious doubt the utility for these taxa of the uniform sets of criteria and fixed benchmarks or thresholds currently being used to assess levels of endangerment (Frederick *et al.* 1996; Pagel and Payne 1996).

The behavioural and ecological adaptations which enable nomadic animals to take advantage of complex resource pulses set them apart from other taxa. Nomads are generally highly colonial, social animals and the behavioural adaptations which facilitate efficient food finding over extensive areas have been associated with large population size (Bucher 1992; Frederick *et al.* 1996; Fahse *et al.* 1998). The minimum population required to locate irregular, distantly located resource pulses is predicted to be substantially higher than that required to maintain either genetic diversity or viability in insular populations or in taxa with regular migration paths. Similarly, the minimum habitat area required to support an individual through its life is significantly greater than for other taxa; and the stochastic nature of resource

production at fine scales makes it impossible to predict and conserve essential habitat areas (Eby 1991; Pressey 1994; Fahse *et al.* 1998). Further, as the relative value of habitat areas change unpredictably through time, incremental shifts in habitat quality can have widespread, largely unforeseeable consequences that cause populations to decline at more rapid rates, over larger areas or with greater lag times than would usually be predicted by the perceived extent of change (Frederick *et al.* 1996).

The difficulties that arise in evaluating the threatened status of nomads can be accommodated to some degree by making assessments during identifiable periods of vulnerability. For example, patterns of migration characteristically include periods of concentration in which an intensive resource flush at a time of general scarcity results in large proportions of a population congregating into restricted areas (Brower and Malcolm 1991). Migratory species are particularly vulnerable in these circumstances. The loss of the comparatively small habitat areas which support the population can have a dramatic and rapid impact, diminishing the usual capacity for large population size and expansive range to reduce extinction risk. Various procedures used to determine threatened status acknowledge this vulnerability and provide for assessments to be made during periods of concentration (IUCN 1994; Lunney *et al.* 1996).

Grey-headed Flying-foxes *Pteropus poliocephalus* are large (600–900 g), nectarivorous and frugivorous bats which are endemic to eastern Australia (Tidemann 1995). They feed in canopy vegetation and have a diverse diet comprising 54 species of flowers, primarily from *Eucalyptus* and related genera and 48 species of fruit produced in subtropical rainforest (Parry-Jones and Augee 1991; Eby 1995, 1996). Grey-headed Flying-foxes have complex and irregular migration patterns which are primarily determined by eruptive pulses of nectar flow produced in a range of forest and woodland communities (Nelson 1965; Eby 1991; Parry-Jones and Augee 1992; Richards 1995). The majority of animals undertake nomadic migrations either continuously or in certain seasons (Eby 1991; Parry-Jones and Augee 1992). Radio-telemetry studies have shown that individuals can locate and move between successive nectar pulses that occur hundreds of kilometres apart (Eby 1991; Spencer *et al.* 1991). The methods used for locating successive stands of flowering trees are not known, although there is evidence of a threshold of flowering intensity below which animals do not migrate to areas of floral production (Eby 1991).

Grey-headed Flying-foxes are highly colonial and roost conspicuously in the branches of canopy trees. The species shares its camps with two other *Pteropus*, the Black Flying-fox *P. alecto* and the Little Red Flying-fox *P. scapulatus*, in areas where their distributions overlap (Webb and Tidemann 1995). With few exceptions, the size of camp populations and their patterns of occupation vary considerably between seasons and between years (Parry-Jones and Augee 1992; Eby 1995).

Grey-headed Flying-foxes are affected by a number of threatening processes throughout their range and are particularly vulnerable to loss or modification of foraging habitat and to culling by humans, which primarily affects pregnant and lactating females (Eby 1995; Tidemann *et al.* 1997; Richards and Hall 1998). Further concerns have been raised regarding competition for foraging resources from Black Flying-foxes (Ratcliffe 1932; Webb and Tidemann 1995). The conservation status of Grey-headed Flying foxes has been assessed nationally as Vulnerable in the *1999 Action Plan for Australian Bats* under IUCN Criterion A2 (c,d,e) (Duncan *et al.*, in press). A reduction in population of at least 20% is projected or expected to be met within the next 10 years or three generations. The case for the listing is primarily based on the projected loss to development of coastal lowland forests on privately-owned land in south-east Queensland and north-east New South Wales. This habitat area is known to support winter population concentrations and its loss will predictably result in a rapid reduction in population (Eby 1996). The listing does not provide enhanced protection for Grey-headed Flying-foxes unless individual states list the species under their threatened species legislation. The distribution of Grey-headed Flying-foxes spans three states, Queensland, New South Wales and Victoria, and the species is currently listed as Vulnerable only in Victoria.

The aim of this study was to provide information relevant to an assessment of the conservation status of Grey-headed Flying-foxes in New South Wales by describing the distribution and abundance of the species at a time when food resources were limited in species composition and distribution, and the population in the state was concentrated into small areas. As the distribution of Black Flying-foxes in New South Wales is restricted to the far north-east corner of the state and occurs entirely within the distribution of Grey-headed Flying-foxes, the study coincidently described the distribution and abundance of Black Flying-foxes which are listed on Schedule 2 (Vulnerable) of the New South Wales *Threatened Species Conservation Act, 1995.*

METHODS

The size and distribution of nomadic populations are most accurately assessed using synchronous surveys in which data are collected over large geographic areas (Frederick *et al.* 1996; Clarke 1997; Garnett *et al.* 1999). A synchronous count of Grey-headed Flying-foxes was taken throughout its range in New South Wales in July 1998. A second synchronous count taken in September 1998 aimed to provide an additional assessment of counting error. The method was structured as a three-stage process which comprised an assessment of the distribution of flying-foxes in New South Wales at the time of the count; synchronous flyout counts of animals at occupied camps; and ground assessments of the size of camp populations, species composition of camps and broad demographic parameters. Flyout counts were conducted by volunteers from non-government organizations such as wildlife care groups and field naturalist groups, and by other interested individuals.

Assessments of distribution

Data on the distribution of Grey-headed Flying-foxes in New South Wales was gathered in the week prior to synchronous counts using three methods: a survey of known or potential areas of nectar flow from diet plants, a survey of sightings of flying-foxes and a survey of known camp sites. Initially, members of the apiary industry were surveyed for information on the locations of current or projected nectar flow from *P. poliocephalus* diet plants. Information was gathered from New South Wales Agriculture Apiary Officers and professional beekeepers working within the range of the species. Areas of nectar flow identified by this method were mapped. While the availability of fruit from subtropical rainforest is at an annual minimum during winter and early spring (Holmes 1987; Innis and McEvoy 1992), significant patches of subtropical rainforest were identified as potential areas of food production for the purposes of this study and were also mapped. Secondly, members of wildlife care groups, field naturalist groups, beekeepers and employees of land management agencies such as New South Wales National Parks and Wildlife Service and State Forests of New South Wales were contacted and asked to survey their local areas for the presence of flying-foxes, particularly sightings of foraging animals. A particular effort was made to survey the locations identified by apiarists and areas of subtropical rainforest. Results from non-targeted areas were biased towards locations visited or occupied by people at night. This method was uneven in its coverage of remote areas. Finally, known camps located in areas identified by the previous methods were visited and inspected for the presence of flying-foxes. All known camps that are inhabited annually by the species were also inspected regardless of whether they occurred near identified areas of food availability.

Flyout counts

The size of the population of occupied camps was assessed by counting the numbers of animals that emerged from camps at dusk. These flyout counts were conducted over two consecutive nights, 4 and 5 July and 5 and 6 September, 1998.

A co-ordinator was delegated to each occupied camp. Co-ordinators took responsibility for organizing a team of volunteers to assess their camp using a uniform method which was provided by the organizers of the count. Results and comments were recorded on standard data sheets. Co-ordinators were selected on the basis of their experience with flying-foxes, experience with and knowledge of local camp sites, proficiency in identifying the three flying-fox species which occupy New South Wales and proficiency in sexing and differentiating between adult and subadult animals in the wild. In most cases co-ordinators had prior experience of flyout counts.

During the day prior to the flyout count an assessment was made of the percentage of animals of each species present in camps. Although *Pteropus* species share camps, they generally segregate within them (Ratcliffe 1932). Co-ordinators searched camps from the ground for trees containing different species and estimated relative percentages. Where less than 500 animals of one species occupied the camp, the result was recorded as a count rather than a percentage. Where possible, co-ordinators were asked to estimate the percentage of adults and subadults in each camp (identifiable by size and behaviour) and the percentage of males and females (identifiable by external genitalia).

Counts

A method for estimating the size of flying-fox camps using flyout counts has been described elsewhere (Thomas and LaVal 1990; Parry-Jones 1993; Garnett *et al.* 1999). The paths taken by flying-foxes when departing from a camp vary between highly dispersed, "fan-like" paths and concentrated streams of flight. Often both are used. Co-ordinators observed departure paths prior to the counting nights to assess the number of counters

required to observe all departing animals and to position them appropriately. Counting stations were then designated between 200 and 400 m from the edge of the camp and their locations were mapped. This distance reduced the potential for multiple counting of those animals that emerged short distances from camps, then doubled back before finally departing for their foraging areas. Counting stations comprised a section of sky which could be observed in a single field of vision, with boundaries which could be defined by visual markers such as emergent trees and artificial structures. At least one volunteer was assigned to each counting station and asked to estimate the total number of animals which passed through their field of vision during the flyout. Data from each volunteer were recorded separately. The time of the commencement of the flyout and its duration were noted, and a general description of the flyout was recorded as were any difficulties encountered in counting departing animals.

In July, the positions taken by volunteers were rotated between the two nights as a method of assessing variance between counters. In September, co-ordinators assigned two people to simultaneously estimate numbers at one or more counting stations, according to the availability of volunteers. The difference between these paired counts was expressed as the percentage deviation from the mean of the counts and was plotted against the mean.

Ground assessments within camps

Three camps ranging in approximate population size from 1 000 to 18 000 were visited during the day of a flyout count to assess the size of the population in the roost. The objectives were to provide a population estimate derived from a separate counting method for comparison with results from flyout counts and to explore the potential for using data on the size of occupied roost trees to predict population size. The diameter at breast height of each roost tree was measured and an estimate made of the number of animals in the tree. In two camps, Bellingen Island and Royal Botanic Gardens Sydney, every roost tree was assessed, while in the Maclean camp data collected along a transect covering approximately 17% of the camp area were used to extrapolate a total.

RESULTS

Assessments of distribution

In the final week of June 1998, the areas of nectar production identified by professional beekeepers were confined to coastal lowland vegetation north of 34°S. Nectar flow was reported from Forest Red Gum *Eucalyptus tereticornis* in small, isolated patches between Ballina and Urunga, from *Melaleuca quinquenervia* and *E. robusta* near Taree and from *M. quinquenervia* in western Sydney (Fig. 1). *M. quinquenervia* and *E. robusta* in streetscape plantings were also flowering in the Sydney area. Beekeepers also reported extensive areas of flowering outside the study area including *E. tereticornis* in coastal lowland forests in the south-east corner of Queensland and Napunyah *E. ochrophloia* along the Paroo River, approximately 500 km west of the known range of Grey-headed Flying-foxes.

The distribution of flying-foxes based on sightings correlated closely to that predicted from information on nectar flow. Sightings in New South Wales were limited to the Sydney area and to restricted sites along the north coast. All sightings were associated with occupied camps. There was no evidence of animals roosting in a dispersed fashion or feeding in areas not associated with communal sites. A total of 62 camps was inspected in the days prior to the July count (Fig. 1). Twelve were occupied. All occupied camps were located within 40 km of the coast and at an elevation of less than 20 m. Their locations reflected the distribution of mapped nectar production and sightings of animals.

In September 1998, the results from all three methods indicated that the distribution of flying-foxes in New South Wales was more dispersed than at the time of the July count. Food resources were available from Yellow Box *E. melliodora* and Blakely's Red Gum *E. blakelyi* in limited areas on the tablelands and from Grey Ironbark *E. siderophloia*, *E. paniculata* and related species, and Forest Red Gum *E. tereticornis* in coastal habitats. Fifteen camps along the coast north from Sydney were occupied. Animals were also sighted on the northern and central tablelands, although the locations of these camps were unknown.

Species composition of camps and assessment of demographic parameters

Grey-headed Flying-foxes were found at 11 of the 12 camps occupied by flying-foxes in July 1998 and Black Flying-foxes were found at 7 of the 12 camps (Table 1). Black Flying-foxes were present in the Maclean camp and in all occupied camps north of this site, but were not found south of Maclean. The percentage of Grey-headed Flying-foxes in shared camps ranged from 98% at Maclean to 0.8% at Currie Park. No Little Red Flying-foxes were recorded in the study area, although it was noted that the species was present in New South Wales, feeding on *E. ochrophloia* west of Bourke.

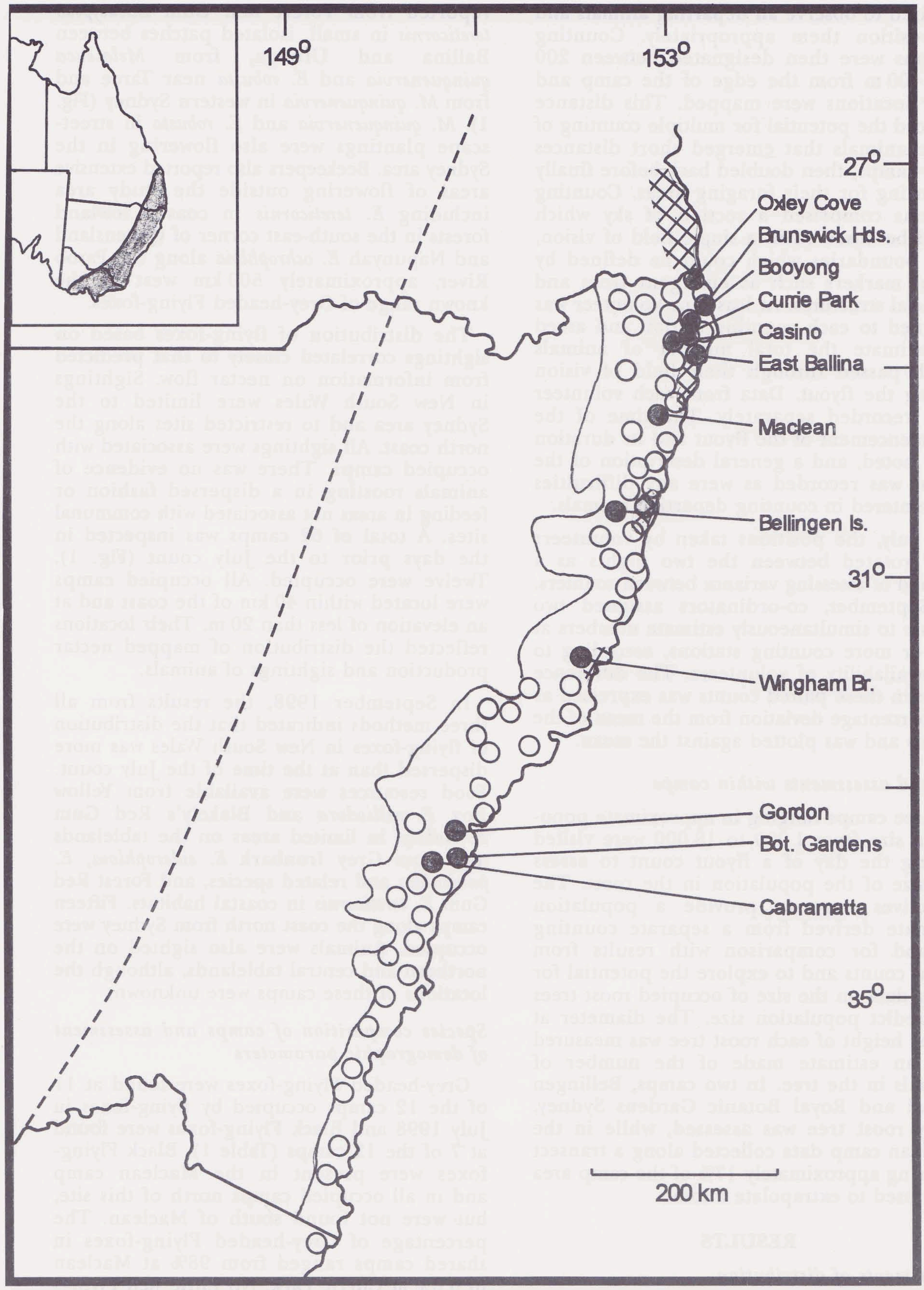

Figure 1. Eastern New South Wales and south-east Queensland, showing the western boundary of the range of Grey-headed Flying-fox (dashed line); the locations of camps in New South Wales occupied at the time of the July count (filled circles); the locations of inspected camps that were empty (open circles); and identified areas of nectar flow (hatched). The western boundary of the coastal botanical region is also shown. It should be noted that the extent of the hatched area is not indicative of the amount of foraging habitat. These landscapes are highly variable. They comprise urban areas and agricultural land as well as highly fragmented, remnant woodlands. Insert = a map of the distribution of Grey-headed Flying-foxes.

Table 1. The numbers of Grey-headed and Black Flying-foxes in New South Wales in July 1998. The results of synchronous flyout counts of flying foxes taken at occupied camps in New South Wales on 4 and 5 July, 1998. Counts are rounded to the nearest hundred. Columns 1 and 2 show the total numbers of flying-foxes of both species counted during two successive evening flyouts; Column 3 shows the percentage of Grey-headed Flying-foxes in each camp, asterisks identify the two camps where these data were used to calculate the numbers of Grey-headed and Black Flying-foxes given in Columns 4 and 5; Column 4 shows the count of Grey-headed Flying-foxes in each camp; Column 5 shows the count of Black Flying-foxes in each camp; Column 6 shows an estimate of the percentage of females in camps; Column 7 shows an estimate of the percentage of sub-adults in camps.

Name of camp site	Total count (both species) 4 July	5 July	% G-h ff	Count G-h ff	Count Bk ff	% female	% subadult
Oxley Cove	n.d.(a,b)	14 800	2	300	14 500		
Brunswick Hds	n.d.(a)	11 200	70*	7 800	3 400		
Booyong	n.d.(a)	7 300	95	6 900	400	60	5
Currie Park	44 800	49 900	0.8	400	49 500		30
Casino	n.d.(c)	200	0	0	200		10
East Ballina	4 100	8 600	50*	4 300	4 300		5
Maclean	13 300	12 000	98	11 800	200	57.4	38
Bellingen Is.	23 900	17 800	100	17 800	0	60	25
Wingham Brush	n.d.(a)	10 800	100	10 800	0		5
Gordon	3 700	3 600	100	3 600	0		
Botanic Gardens	1 200	1 100	100	1 100	0	65	20
Cabramatta	n.d.(b)	20 600	100	20 600	0		10
Totals		157 900		85 400	72 500		

n.d. = no data; (a) = count affected by poor visibility; (b) = count affected by insufficient counters; (c) = count taken by ground assessment.

All camps occupied by Grey-headed Flying-foxes contained mixed groups of adult males, adult females and sub-adults of both sexes. Adult males and females were interspersed through the camps, sharing roost trees, while sub-adults roosted in separate even-age groups. Estimates of the percentage of sub-adults in camps varied between 5% and 38%. Estimates of sex ratios proved difficult to achieve and were made at four camps only. Estimates of the percentage of females in these camps ranged from 57.4% to 65%.

Counts

Flyout counts were conducted at 11 occupied camps. The twelfth site, Casino, had so few animals that they could be counted from the ground. Poor weather conditions on the night of 4 July, including low cloud cover and rain, reduced visibility at dusk and prevented accurate counts from being made at four camps. However, the night of 5 July was clear and results from this night were taken as final counts. The total count of flying-foxes in New South Wales taken on 5 July was 157 900, comprising 85 400 Grey-headed Flying-foxes and 72 500 Black Flying-foxes. The size of camp populations ranged from 200 to 49 900; median = 11 000. Both species were highly concentrated: 99.2% of Grey-headed Flying-foxes occupied nine camps and 93.7% occupied seven camps; 99.4% of Black Flying-foxes occupied five camps, 88.3% occupied two camps and 68.3% occupied one camp.

The nightly totals from individual counting stations ranged from 123 to 8 840 (median = 1 610) and varied substantially within camps. This indicates that departing animals used a combination of highly dispersed paths and concentrated flight streams. There was evidence from areas unaffected by poor weather on 4 July that the numbers of animals flying over counting stations varied substantially between nights, either due to shifts in flight paths or due to actual changes in the size of camps. For example, the count at station 5 at Bellingen Island was 7 700 on night 1 and 400 on night 2. Similarly, counts on successive nights at station 4 at the Ballina camp were 140 and 1 830 and counts on successive nights at station 5 were 110 and 2 800. At Bellingen Island, the change in total count from 24 000 on night 1 to 17 800 on night 2 coincided with an observed decrease in the numbers of trees occupied within the camp and was interpreted as an actual reduction in the size of the camp population. Conversely, the increase from 4 100 to 8 600 at Ballina was interpreted as an actual increase in numbers. As a result of nightly changes in both population size and the direction of flight streams, data collected over consecutive nights could not be used to estimate deviation between counters, so data from paired counts were used for this assessment.

The results of 24 paired counts suggest a low level of deviation between counters (Fig. 2). With one exception, the percentage deviation around the mean was less than 13%, with a mean of 8.4%. The results further suggest that levels of deviation between counters did not alter with increasing size of counts up to 8 000. Further data are required to confirm this result.

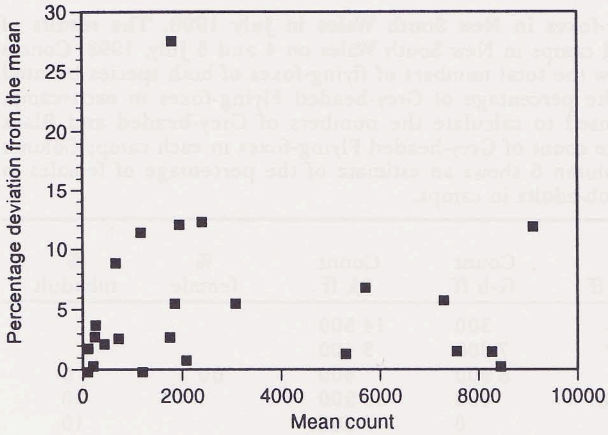

Figure 2. An assessment of variance in the flyout counts taken by individual counters, expressed as the relationship between the mean value of paired counts and the percentage deviation from the mean.

Flyout commenced between 17:21 and 17:35 Eastern Standard Time (EST) in July and between 17:55 and 18:04 EST in September and lasted from 13 to 29 minutes. No relationship was found between the size of a camp population and the duration of the flyout (Fig. 3). The flyout at Currie Park with a population of 49 900 was of the same duration as the flyout at the Royal Botanic Gardens with a population of 1 100.

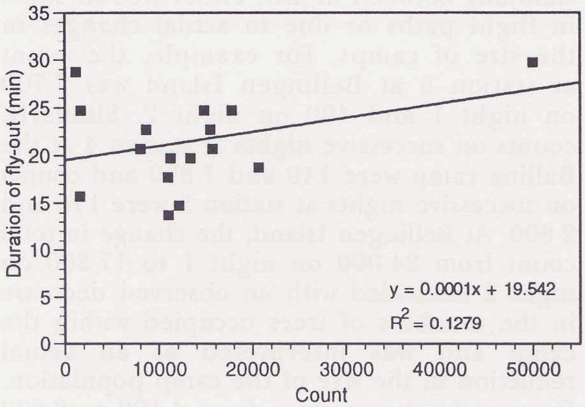

Figure 3. The relationship between the duration of the flyout from 16 Flying-fox camps in New South Wales and the estimated size of camp populations.

Ground assessments within camps

Ground assessments were found to be of limited use in estimating the size of the camps occupied during July. The procedure was not appropriate for camps which were rarely visited by humans and therefore contained animals that were easily disturbed, camps where access was prohibitive or camps where the density of canopy vegetation reduced the visibility of roosting animals. As a result, ground estimates were made in three camps only. The relationship between abundance estimates made using this method and estimates made using flyout counts was variable. The ground estimate of 11 935 taken at Bellingen Island was 33% lower than the flyout count; the ground estimate of 12 162 taken at Maclean was equivalent to the flyout count (+0.7%); and the ground estimate of 1 740 taken at the Royal Botanic Gardens in September was 12% higher than the flyout count.

There was no indication that data on the diameter of roost trees could be used to predict the size of a camp population with acceptable accuracy (Fig. 4). Estimates of numbers of animals occupying trees of DBH less than 50 cm ranged from 5 to 100 and numbers in trees greater than 50 cm ranged from 20 to 300.

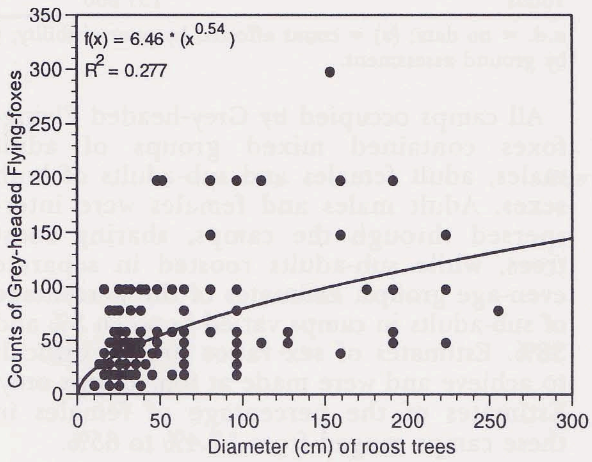

Figure 4. The relationship between the diameter at breast height of roost trees (n = 183) and counts of roosting Grey-headed Flying-foxes.

DISCUSSION

In July 1998 the foraging resources for flying-foxes in eastern New South Wales were available in restricted habitat patches in coastal lowland vegetation and Grey-headed and Black Flying-foxes were congregated in a small number of camps associated with these resources. This concentration of animals during a period of general resource scarcity presented an opportunity to assess the abundance and distribution of Grey-headed Flying-foxes at a time when the species was vulnerable to loss of critical winter habitat. We argue that these were appropriate circumstances in which to examine the conservation status of the species in New South Wales. The data additionally provided a point of comparison with earlier evaluations of the distribution and abundance of flying-foxes in the state.

Level of error and confidence in results

This was the first attempt at a synchronous survey of flying-foxes in New South Wales. There are inherent difficulties in conducting broad-scale surveys such as this, and the accuracy and certainty of the outcome were contingent on our capacity to locate the animals, estimate the percentage of individual species in shared camps and count the camp populations. Our method addressed the first of these issues by employing three techniques for identifying the location of flying-foxes. We consider that the inherent error in this stage of the counting procedure is low and propose that the results accurately reflect the distribution of flying-foxes at the time of the July 1998 count. There is no evidence from our survey of beekeepers that alternative floral sources were available within the New South Wales range of Grey-headed Flying-foxes, nor were animals sighted in areas not targeted by nectar mapping. Although we did not incorporate into our design a method for assessing error in estimates of the percentage of species in shared camps, it should be noted that this potentially influenced the results from only two camps. In the other four camps which were shared, the numbers of either Grey-headed or Black Flying-foxes were less than 500. This was sufficiently low to be assessed by counting individual animals prior to the flyout. We also regard the level of error introduced at this stage to be relatively low.

It will not be possible to assign error values to our count data without a significant number of repeat counts. Although it has been proposed that large numbers of bats can be accurately estimated as they emerge from communal roosts (Thomas and LaVal 1990), a substantial body of data is required to validate abundance estimates and to model error structure. Nonetheless, we gathered data pertinent to a preliminary evaluation of counting error by assessing variance between individual counters and by comparing the estimates obtained from flyout counts with those obtained from ground assessments. The percentage deviation between paired counts provided the best evidence of the relative accuracy of individual counters. Levels of deviation described by this method were surprisingly low and remained uniform as the numbers of animals counted increased. This result suggests that synchronous flyout counts can be used to monitor population trends. It also supports a degree of confidence in the absolute abundance figures.

Ground assessments proved to be of limited value in providing comparative data for an assessment of bias in flyout counts. Although Ratcliffe (1932) suggested that flyout counts consistently over-estimate the size of camp populations relative to ground assessments, abundance estimates derived by the two methods in this study varied substantially between camps and did little to illuminate the relative bias in these methods. We attribute this variation to differences between camps in the density of canopy vegetation and, therefore, the visibility of roosting animals. The vegetation at Bellingen Island, where the abundance estimate from the ground assessment was 33% less than from the flyout count, has a relatively dense canopy which could have reduced the ability of the counter to sight roosting animals. Conversely, the vegetation at Maclean, where abundance from the two methods was equivalent, had an open canopy at the time of the count which would have left roosting flying-foxes exposed to view.

Comparisons with earlier work

Although the level of error associated with flyout counts remains undefined, the magnitude of the difference between our results and other appraisals of the abundance of Grey-headed Flying-foxes demonstrates that the size of the current population has previously been significantly over-estimated (Parry-Jones 1993; Richards and Hall 1998). On the basis of work conducted on the central and southern coast of New South Wales, Parry-Jones (1993) predicted that camps of 20 000 Grey-headed Flying-foxes occurred at approximately 35 km intervals, and that the total population of the state was one million. Similarly, Richards and Hall (1998) assumed a uniform population size of 50 000 at 40 camps and proposed a basal population size for the species of two million. Each of these estimates is contingent on an assumption that resource availability for Grey-headed Flying-foxes is relatively homogeneous over large spatial scales and that camp populations are therefore uniform. However, this assumption is not supported by nectar mapping over several years (Eby 1996), by informal observations of the distribution and abundance of Grey-headed Flying-foxes in New South Wales (P. Eby and K. Parry-Jones, pers. obs.), by monthly surveys in Queensland (P. Birt, University of Queensland, unpubl. data) or by the results of this study. Rather, the distribution of foraging resources, and therefore the distribution of animals, is uneven and highly variable. Consequently, estimates of total abundance are most reliably made by synchronous field assessments.

It is possible that this study documented a period when the number of Grey-headed

Evening flyout of Grey-headed Flying-foxes from Bellingen Island in the Bellinger River, New South Wales. This is the main stream of a flyout which commences shortly after sunset and typically lasts 13 to 29 minutes. Counts of emerging animals are made using a visible frame of reference created by trees and power lines. On 5 July, 1998 Grey-headed Flying-foxes occupied 11 camps in New South Wales. The total number in the state was estimated from a synchronous flyout count to be 85 400. This number is considerably lower than any previous assessment. The decline in population of Grey-headed Flying-foxes is attributed to ongoing clearing of critical over-wintering habitat in low-lying coastal woodlands. The results from this study support their listing as a vulnerable species in the *1999 Action Plan for Australian Bats.*

Flying-foxes in New South Wales was exceptionally low and that sufficient numbers of this mobile species were resident in Queensland and Victoria at the time of the July 1998 count to substantiate an abundance estimate of two million. However, the available evidence does not support this view. The New South Wales count coincided in its timing with a monthly assessment of the distribution and approximate abundance of flying-foxes taken in south-east Queensland (P. Birt, unpubl. data). As in New South Wales, Grey-headed Flying-foxes in Queensland were congregated in camps in the coastal lowlands at the time of the July count, and, in keeping with reports of nectar flow from New South Wales beekeepers, were primarily located within 100 km of Brisbane. Their abundance was estimated at approximately 300 000 (P. Birt, unpubl. data). The animals were known from a single camp in Victoria, whose size was estimated at 5 000 (I. Temby, pers. comm.), giving a total abundance estimate for the species of *ca* 400 000. The methods used to estimate abundance in Queensland and Victoria differed from our methods and did not include an estimation of error. Therefore, this figure must be considered indicative. However, we regard these data to represent the most accurate estimation of the total abundance of Grey-headed Flying-foxes currently available.

These results support the widely-held view that the population of Grey-headed Flying-foxes has declined substantially since the time of European settlement (Ratcliffe 1932; Eby 1995; Lunney *et al.* 1996; Lunney and Moon 1997; Richards and Hall 1998). While the historical accounts on which this view is based are largely descriptive, they provide clear qualitative evidence of a substantial decline in population (Ratcliffe 1932; Lunney and Moon 1997). By the time the first assessment was made of the abundance and distribution of Australian flying-foxes in the late 1920s, the pre-European population of Grey-headed Flying-foxes had reportedly halved and the remaining population of flying-foxes in eastern Australia was estimated at "many millions" (Ratcliffe 1932). A decline in the New South Wales population has been inferred from changes in the sizes and frequencies of current camps relative to accounts from earlier this century (Lunney and Moon 1997). These changes have been attributed to the cumulative impact of habitat loss, shooting and increasing competition for diminishing resources from Black Flying-foxes (Ratcliffe 1932; Lunney and Leary 1988; Eby 1995; Webb and Tidemann 1995; Tidemann *et al.* 1997).

Competition with Black Flying-foxes

Competition for resources between Black and Grey-headed Flying-foxes has been inferred from an ongoing expansion of the southern distribution of Black Flying-foxes into coastal areas inhabited by Grey-headed Flying foxes (Eby 1995; Webb and Tidemann 1995). The distribution of Black Flying-foxes underwent a substantial southerly shift between the time it was first described in the 1920s and the early 1960s, from the Mary River in Queensland to the Tweed River in New South Wales (Ratcliffe 1932; Nelson 1965). However, the southern limit to the distribution was not precisely defined by Nelson (1965) and evidence of a further southerly shift is tenuous. Nelson (1965) found the species in camps in the Tweed Valley, but not in the next southerly camp he inspected which was at Grafton, New South Wales. Nelson did not report the species compositions of camps between the Tweed River and Grafton. It remains the case that Black Flying-foxes inhabit camps in the Tweed Valley (e.g., Oxley Cove) and do not inhabit the camp on Susan Island at Grafton (Eby and Palmer 1991; P. Eby, unpubl. data). In the late 1980s, East Ballina, which was not inspected by Nelson (1965), was recorded as the furthest southerly camp used by the species (Eby and Palmer 1991). While in this study they were recorded 80 km further south at Maclean, it should be noted that the camp at Maclean was not inhabited by flying-foxes during the late 1980s due to a programme of licensed culling, and camps located between Ballina and Maclean were not surveyed for Black Flying-foxes during this time (P. Eby, unpubl. data). Thus there is no firm evidence of a shift in the distribution of Black Flying-foxes since the 1960s. However, the July 1998 count did indicate that the ratio of Black Flying-foxes relative to Grey-headed Flying-foxes in shared camps has increased over the past ten years. This shift is most clearly demonstrated by data from the Currie Park camp. In February 1988, approximately 95% of 45 000 animals counted in the camp were Grey-headed Flying-foxes (Eby and Palmer 1991), while in July 1998, 99% of the 49 900 animals counted were Black Flying-foxes.

Vulnerability to habitat loss

Winter is a period of general food scarcity for Grey-headed Flying-foxes. Few diet plants have winter flowering schedules and the volume of ripe fruit produced in subtropical rainforest is at an annual minimum (Holmes 1987; Innis and McEvoy 1992; Eby 1996). However, the plants that flower in winter produce carbohydrate-rich nectar and pollen

high in protein content, and can provide abundant resources in small habitat areas (Clemson 1985; Stace 1996). Although the spatial distribution of winter nectar flow follows broad rules on a regional scale, the small-scale configuration of flowering which defines actual distribution and abundance patterns is irregular and constrained by the supra-annual flowering patterns of local plant populations, many of which are productive less than one year in three (Sommerville and Dodds 1995; Sommerville and Rienstra 1997; Sommerville and Robertson 1997). Long-term mapping of nectar flow in relation to animal abundance shows that abundant winter resources in New South Wales are produced by White Box *E. albens* in association with various ironbarks on the northwestern slopes every third year, and by single species stands of Spotted Gum *Corymbia maculata* on the far south coast approximately one year in five (Eby 1996). However, more reliable resources are produced in lowland coastal woodlands in northern New South Wales and in southern Queensland dominated by *E. tereticornis, E. robusta, M. quinquenervia* and *Banksia integrifolia* (Clemson 1985; Pressey and Griffith 1992). In approximately 30% of years the only significant winter foraging resources available in New South Wales occur in coastal woodlands at low elevations and large numbers of flying-foxes congregate in these areas, as illustrated by this study. Grey-headed Flying-foxes are known to migrate from camps many hundreds of kilometres away to utilize these winter resources (Eby 1991).

The reliance of Grey-headed Flying-foxes on small areas of coastal woodlands demonstrates their vulnerability to further population reductions from the loss of critical over-wintering habitat, and lends further support to the case for listing this specie as Vulnerable in the *1999 Action Plan for Australian Bats* (Duncan *et al.*, in press). Coastal vegetation communities dominated by *E. tereticornis, M. quinquenervia* and *E. robusta* in northern New South Wales and southern Queensland occur predominantly on freehold land, and their conservation is threatened due to their poor reservation status and the predicted impacts of clearing for coastal development (Pressey and Griffith 1992; Pressey *et al.* 1996; Norton 1996; Queensland Regional Forest Assessment Steering Committee 1997). As a direct result of ongoing, exponential increases in the human population in these areas, remnant native vegetation is being cleared for urban and semi-rural development (Catterall *et al.* 1997; Regional Planning Advisory Group 1994; New South Wales Department of Planning 1995). Clearing is asymetrical, predominantly affecting lowland, coastal vegetation on freehold land (Pressey *et al.* 1996; Catterall *et al.* 1997). Data on projected rates of human immigration and the locations of current and planned centres of development in south-east Queensland have been used to project the impact of this phenomenon on remnant vegetation in that state, including rates of clearing of different vegetation types (Catterall and Kingston 1993; Regional Planning Advisory Group 1994; Catterall *et al.* 1997). Catterall *et al.* (1997) estimate that at current rates of clearing, all remnant stands of lowland eucalypt woodlands of greater than 10 ha or greater than 100 m width that are outside protected areas will be cleared by between 2016 and 2040. Data on projected rates of clearing in New South Wales have not been compiled; however, similar patterns of change are predicted in lowland vegetation along the north coast (Pressey *et al.* 1996; Catterall *et al.* 1997). Ongoing reduction of this habitat will substantially diminish over-wintering resources for the mobile nectarivores of temperate and subtropical eastern Australia (Nix 1993; Catterall *et al.* 1998). Any increase in the proportion of Black Flying-foxes inhabiting these areas will amplify the effect on Grey-headed Flying-foxes. The size of the current population will not protect it from the projected impact of this threatening process nor will its expansive distribution.

Grey-headed Flying-foxes are additionally impacted by incremental reductions in food availability throughout their range as a result of forest clearing and degradation, forestry practices, eucalypt dieback, drought, fire and the vulnerability of nectar flow to fluctuations in temperature and rainfall (Norton 1996; House 1997). That 82% of the plants in their diet list occur either in lowland coastal areas or on fertile soils away from the coast supports the contention that the species relies on vegetation communities that are prone to clearing for development and agriculture, and are poorly served by systems of forest reserves in eastern Australia (Eby, unpubl. data; Pressey *et al.* 1996; Catterall *et al.* 1997). The irregular nature of fine-scale habitat use by Grey-headed Flying-foxes makes it impossible to project a rate of population reduction from these largely undocumented processes. However, they significantly increase extinction risk in this migratory species (Frederick *et al.* 1996; Pagel and Payne 1996; Fahse *et al.* 1998).

The difficulties that exist in assessing the threatened status of nomads are particularly pertinent to wildlife conservation in eastern Australia where nomadism has been identified

or inferred in a number of forest-dwelling nectarivorous birds and bats (Ratcliffe 1932; Keast 1968). The need to conserve continuous nectar flow at appropriate spatial scales for these species has been acknowledged as an important concept in forest conservation in Australia, and the impact of reductions and alterations in forest habitat on the status of these species is an area of growing concern (Woinarski *et al.* 1992; Nix 1993; Eby 1995; Norton 1996; Catterall *et al.* 1998). Our capacity to adequately manage mobile nectarivores is inhibited by a lack of information and inadequate understanding of the complex, irregular resource systems they inhabit. Nomadic species are poorly studied, due primarily to the conceptual and logistical impediments associated with acquiring significant data sets over large spatial scales (Clarke 1997). In particular, trends in the abundance of nomads are difficult to monitor directly given their fluid and unpredictable patterns of distribution. Synchronous censuses taken over expansive areas are the most widely accepted method for monitoring population trends in these species (Frederick *et al.* 1996). However, the scale of such censuses make them rare events (Thomas and LaVal 1990; Clarke 1997). To acquire the data presented in this paper required significant efforts of over 150 volunteers. Our experience suggests that it is possible to develop a network of volunteers to conduct flyout counts in a rigorous fashion. However, the effort required to monitor population trends, assess error and validate estimates of absolute abundance are unlikely to be sustained outside a formal structure. We recommend that conservation management agencies in New South Wales, Queensland and Victoria work co-operatively to support and co-ordinate regular synchronous counts of flying-foxes.

ACKNOWLEDGEMENTS

We are indebted to P. Birt from the University of Queensland for her permission to quote unpublished data on abundance estimates in that state and to I. Temby for data from Victoria. We also thank S. Garnett, B. Law and an anonymous referee for helpful comments on an earlier draft of this manuscript. B. White, D. Sommerville, and J. Rhodes from New South Wales Agriculture kindly provided information on flowering patterns as did several professional beekeepers. This project clearly relied on the substantial goodwill and efforts of a large number of volunteers who searched for foraging animals, surveyed camp sites and participated in counts. We would particularly like to thank the co-ordinators who organized counting teams and kept such comprehensive records. Their names are emboldened in the following list. I. Preston, J. Manning, K. Alley, A. Rodgers, A. Jones, A. Seddon, **A. Boardman**, A. Smith, A. Taylor, A. Coyle, A. Johansson, A. Farber, A. Webb, A. Bunn, A. May, B. Clay, B. Beshaw, B. Dowling, B. Sansom, B. Davies, **B. Oehlman**, B. Bricknell, B. Lunney, B. Edwards, B. Sharp, B. Taylor, C. Rodgers, C. Jackett, C. Pountain, C. West, C. Eggert, C. Cochran, C. Kilgour, C. Leigh, C. Moon, C. Hannah, D. Kilgour, D. Bidwell, D. Charlie, D. Tregillas, D. Wood, D. Newel, **D. Ford**, D. Davies, E. McGregor, **E. Gough**, G. Taylor, G. Opit, **G. Bennett**, G. Storrock, G. Maisey, G. Rheinberger, **H. Meddick**, H. Naylor, H. Bartle, H. Nicholson, I. Urosevic, **I. Selby**, **J. Maisey**, J. Tregillgas, J. Storrock, J. Kilgour, J. Bricknell, J. Schell, J. Lunney, J.Woodmore, J. Kelly, J. Gough, J. Kosakoff, J. Rabbitt, J. Mclean, J. Richards, K. Joynes, K. Black, K. Ulyait, K. Maude, K. Moran, K. Robertson, K. Wyborn, L. Williams, L. Johnson, L. Webb, L. Doherty, L. Reed, L. McDermott, L. Stevenson, L. Veal, L. Truswell, L. Black, L. Hardman, L. Ives, L. Rowe, L. Jephcott, M. Outerbridge, **M. Sansom**, M. Kerr, M. Boshaw, M. Moran, M. Heggie, M. Bull, **M. Beck**, M. Fisher, M. Bullock, M. Luscombe, M. Ryan, M. Byrne, M. Clay, M. Cochran, M. Fleming, M. Collins, M. Wyborn, M. Alfred, **M. Davies**, M. Munro, N. Nicholson, N. Weeks, N. Drinkwater, N. Smith, N. Gordson, **N. Williams**, N. Bennett, P. Coleman, P. Whitehead, P. McGregor, P. Meddick, P. Murphy, P. Turner, P. Berrill, **R. Rayward**, R. Whittling, R. Bartle, R. Kilgour, R. Rabbitt, **R. Gough**, R. Westbrook, R. Beck, R. Sharp, R. Lord, R. Griffith, R. Leigh, S. Byrne, S. Anderson, S. Swindall, S. Faun, S. Stanvic, S. Wyborn, S. King, Sweeney, T. Mather, V. Maude, V. Place, V. McDonald, **V. Jones**, W. Thomas, W. Forbes, W. Riches, Y. Jenkins. We apologize to anyone whose name has been inadvertently omitted.

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